SIEVE-ELEMENT PLASTIDS AND SYSTEMATIC RELATIONSHIPS OF RHIZOPHORACEAE, ANISOPHYLLEACEAE, AND ALLIED GROUPS[1]

H.-Dietmar Behnke[2]

ABSTRACT

One hundred fifty-five species of 41 families belonging to the proposed ordinal composition around and including the families Rhizophoraceae and Anisophylleaceae have been studied with respect to their sieve-element plastids. The great majority of taxa, including the Anisophylleaceae, contain S-type plastids. P-type sieve-element plastids were found in Humiriaceae, Rhizophoraceae, and Erythroxylaceae (all with specific subtype-P5), and (with P-forms not readily assigned to a specific subtype) in Eucryphiaceae, Neuradaceae, Oxalidaceae (s.l.), Rhabdodendraceae, and part of Zygophyllaceae. A critical evaluation of sizes and specific contents of their sieve-element plastids negates close relationships between Rhizophoraceae and Anisophylleaceae, integrates the Rhizophoraceae in the Geraniales, but is not able to suggest a position for the Anisophylleaceae. Within the Geraniales the family sequence Humiriaceae (form-P5cs plastids) –Erythroxylaceae (P5c) –Rhizophoraceae (P5c) is proposed to be paralleled by another P-type containing sequence Lepidobotryaceae (S-type) – Hypseocharitaceae (S) –Oxalidaceae (S, Pc) –Averrhoaceae (Pcfs), both being linked to the S-type Linaceae s.l. Sieve-element data do not support the inclusion of Rhizophoraceae in the Celastrales; however, such data corroborate the exclusion of the new celastralean family Elaeocarpaceae from the Malvales. Among the taxa proposed by Dahlgren, Anisophylleaceae would be best placed in vicinity to the S-type families of the Rosales, not in close association to P-type Neuradaceae. The presence of P-type sieve-element plastids in Zygophyllaceae, Neuradaceae, and Humiriaceae is reported here for the first time.

The family Rhizophoraceae is distinct from other dicotyledon taxa by the formation of rather extraordinary P-type sieve-element plastids (Behnke, 1982a). Their specific form-P5c plastids contain some twenty more or less rectangular protein crystals—i.e., an accumulation of proteins to a degree found nowhere else in P-type plastids—and were originally reported for seven species of the family and an additional four species of the Erythroxylaceae. A closely related form-P5cf (containing protein filaments in addition to the crystals) was found in the family Cyrillaceae (*Cliftonia* and *Cyrilla*). These unique subtype-P5 plastids raised questions about the systematic position of the three families (Behnke, 1982a) and initiated further research on sieve-element plastids and other characters.

A first study of the distribution of types of sieve-element plastids of Myrtales and allied groups (an association of taxa into which the family Rhizophoraceae had been placed most commonly) revealed that (1) all core families of the Myrtales and all of those closely related contained S-type plastids, and (2) within the Rhizophoraceae (an additional seven species were investigated) the two genera *Anisophyllea* and *Combretocarpus* also contained S-type plastids (Behnke, 1984). This gave support to various efforts to separate the tribe Anisophylleeae from the Rhizophoraceae and to erect the family Anisophylleaceae (Cronquist, 1981; Dahlgren, 1983; Tobe & Raven, 1987).

The present additional report on sieve-element plastids in Rhizophoraceae, Anisophylleaceae, and allies is an extension of the previous investigations taking also into account all the higher taxa, i.e., ordinal compositions and their associates, to which the two families have been affiliated (see Dahlgren, this volume).

Materials and Methods

One hundred fifty-five species of 41 families, all proposd by Dahlgren (this volume) for placement around Rhizophoraceae and Anisophylleaceae were investigated (see Table 1).

Living material recently removed from the plant or shipped within a few days under special care is a prerequisite for a fixation of sieve elements and the eventual investigation of their plastids with the transmission electron microscope. Thin hand sections were made with a razor blade from preferably young herbaceous shoots or end parts of tree branches less than 1 cm in diameter. The sections were immersed into a fixing solution containing formaldehyde and glutaraldehyde and processed according to standard methods (see Behnke, 1982b). Material made available by collections at original

locations was sent to Heidelberg either fresh (causing a delay of up to a week between sampling and start of fixation) or as formaldehyde/glutaraldehyde prefixed hand sections (causing an equally long delay between primary and postfixation).

Results

A short outline of characters of sieve-element plastids used to characterize the taxa investigated

Sieve-element plastids are separated into two *types* by presence (P-type) or absence (S-type) of protein crystals and/or filaments, while starch grains may or may not be present. *Subtypes* of P-type sieve-element plastids are identified by any unmistakable feature of their protein inclusions, e.g., the subtype-P5 by a high number of generally rectangular protein crystals. *Forms* of sieve-element plastids are defined by any combination of the three inclusions: c = protein crystals, f = protein filaments, s = starch grains, e.g., P5cf. In addition, all sieve-element plastids within a family will be characterized by their average diameter and average amount of protein vs. starch content (Table 2), both calculated from the respective data of the different species listed in Table 1.

Recent studies of the sieve-element plastids of the Acanthaceae (Behnke, 1986a) and within all families of the Magnoliidae (Behnke, 1988)—the latter for the first time taking into account diameters and quantitative data of the plastids—resulted in a general model for the interrelationships between the different forms of plastids. It was concluded that at least in these groups, P-type plastids may have derived from S-type plastids (for details see Behnke, 1988, but compare with Behnke, 1981).

In his summary statement of Rhizophoraceae and Anisophylleaceae and their systematic relationships, Dahlgren (this volume) proposes a revised classification and lists the ordinal composition around each of the two families. The following description of the sieve-element plastids in these taxa follows his sequence of families.

Distribution of the different sieve-element plastids among the families grouped around Rhizophoraceae

Zygophyllaceae (ZYG; Fig. 1: *Guaiacum, Larrea*). Five species in four genera investigated, one with P-type, the others with S-type plastids. Plastid diameter is 1.2 μm. *Larrea divaricata* contains form-Pcs sieve-element plastids with two protein crystals of different diameters (0.4 and 0.3 μm) and different crystal spacing. There are about

five typically disc-shaped starch grains in addition. The S-type plastids of other species studied contain up to ten starch grains of different diameters and shapes, including typically disc-shaped ones.

In this family the plastids of the mature sieve element are often disrupted, making it impossible to record some protein crystals. Therefore, after the detection of P-type plastids in both collections of *Larrea* (Table 1), all species have been studied once more.

Nitrariaceae (NIT; Fig. 1: *Nitraria*). This monogeneric family, represented here by *Nitraria retusa*, contains S-type plastids with characteristics slightly different from those of ZYG, i.e., with a diameter of 1.0 μm and about five more or less globular starch grains.

Peganaceae (PEG; Fig. 1: *Peganum*). *Peganum harmala* likewise contains S-type plastids with a diameter of 1.2 μm and about five starch grains.

Balanitaceae (BLT; Fig. 1: *Balanites*). Two species investigated in the monogeneric family both contain S-type plastids with about ten globular starch grains. Plastid diameters are 1.7 μm in one and 1.1 μm in the other (Table 1).

Vivianiaceae (VIV; Fig. 1: *Caesarea*). *Caesarea albiflora* contains S-type plastids with up to five typically disc-shaped starch grains. Plastid diameter is 1.1 μm. (See also Behnke & Mabry, 1977.)

Geraniaceae (GER; Fig. 1: *Pelargonium*). Five species in three genera investigated, all with S-type plastids. There are about five disc-shaped starch grains within a plastid, the average diameter of which is 1.2 μm (range 1.0–1.6 μm). (See also Behnke & Mabry, 1977.)

Ledocarpaceae (LDC; Fig. 1: *Wendtia*). *Wendtia gracilis* contains small S-type plastids (diameter 0.9 μm) with a few starch grains of variable sizes. The plastids appear distinctly different from those of the Geraniaceae.

Ixonanthaceae (IXO; Fig. 2: *Ixonanthes*). The two species of *Ixonanthes* investigated contain S-type plastids of an average diameter of 1.1 μm and with an average of ten small and large, more or less globular starch grains.

Humiriaceae (HOU; Fig. 2: *Humiria, Endopleura, Sacoglottis*). Four species in three genera investigated: all with P5cs sieve-element plastids. This form is characterized by numerous (average more than ten) irregular to rectangular protein crystals and about ten small starch grains.

The average measurements are: plastid diameter 1.2 μm and protein crystals 0.3 μm.

Hugoniaceae (HUG; Fig. 2: *Indorouchera*). The two species investigated represent two genera, and both contain S-type plastids with about ten starch grains, among them one or two large ones. The average plastid diameter is 1.1 μm.

Erythroxylaceae (ERX; Fig. 2: *Erythroxylum*). The four species of *Erythroxylum* investigated are characterized by P5c sieve-element plastids. This highly specific form contains about ten up to 0.7 μm large rectangular protein crystals (and no starch), which are densely packed within the comparatively small plastids (diameter 1.1 μm). (See also Behnke, 1982a.)

Linaceae (LIN; Fig. 2: *Linum*). Three species in two genera investigated, all containing S-type plastids with an average of about five starch grains (often including a large globular one), which may disintegrate into small particles. The average plastid diameter is 1.2 μm (range 1.0–1.5 μm).

Lepidobotryaceae (LPB; Fig. 2: *Lepidobotrys*). The monotypic *Lepidobotrys staudtii* contains S-type plastids with up to ten starch grains disintegrated into small particles. The plastid diameter is 1.2 μm.

Oxalidaceae (OXL; Fig. 3: *Averrhoa, Oxalis, Sarcotheca*). Twelve species in five genera investigated. Sieve-element plastids not uniform: two types including three different forms occur in the family.

Averrhoa and *Sarcotheca* contain form-Pcfs plastids with an average diameter of 1.1 μm. This P-form, not specified to belong to a distinct P-subtype, contains protein filaments (f), two rectangular or cubic protein crystals (c) up to 0.4 μm in diameter, and about five globular starch grains (s), of which one may be very large.

Oxalis (8 species tested) is characterized by very small (average diameter 0.8 μm) form-Pc sieve-element plastids with two protein crystals, a very prominent (diameter about 0.5 μm) cubical one and a second, smaller one.

Biophytum and *Hypseocharis* contain S-type plastids of different sizes and different starch contents (see Table 1 and Behnke, 1982c).

Form-Pcfs and -Pc sieve-element plastids (and/ or -Pcs not found in the Oxalidaceae) are reported in other dicots, e.g., in Vitaceae, Rhabdodendraceae, Connaraceae, Eucryphiaceae, Acanthaceae, Gunneraceae (Behnke 1974, 1976a, 1982c, 1985, 1986a, b), and Neuradaceae (see below).

TABLE 1. Sieve-element plastid data of the investigated species. Family = families recognized by Dahlgren (this volume), family acronyms after Weber (1982); D'1989 = number of family in Dahlgren (in press) and family acronym if different from "family"; Herbarium = deposit of vouchers. The following data characterize the sieve-element plastids: Type (and form); DIA = diameter in µm; N = number of protein crystals; PMA = maximum diameter of protein crystals in µm; SN = average number of starch grains. "Publication" refers to previous works of the author.

Family	D'1989	Species	Origin of Material	Herbarium	Type	DIA	N	PMA	SN	Publica-tion
ZYG	236	Guaiacum coulteri A. Gray	BG-HEID	HEID	S	1.2	0	0	8	
ZYG	236	Guaiacum officinale L.	BG-B, -HEID	GH-B, HEID	S	1.3	0	0	8	
ZYG	236	Larrea divaricata Cav.	Mexico, Ulrich, BG-HEID	HEID	Pcs	1.1	2	0.4	5	
ZYG	236	Porlieria hygrometa Ruiz. & Pav.	BG-CP		S	1.2	0	0	8	
ZYG	236	Zygophyllum sp.	BG-HEID	HEID	S	1.5	0	0	5	
NIT	238	Nitraria retusa Aschers.	Israel, J. Aronson		S	1.0	0	0	6	
PEG	237	Peganum harmala L.	BG-E		S	1.2	0	0	5	
BLT	244	Balanites aegyptiaca Delile	BG-L	HEID	S	1.7	0	0	10	
BLT	244	Balanites angolensis	BG-CP		S	1.1	0	0	10	
VIV	240	Caesarea albiflora Cambess.	Brazil, A. Schultz	HEID	S	1.1	0	0	5	(1977)
GER	239	Erodium malachoides Willd.	Italy, H.D.B. 830407	HEID	S	1.0	0	0	5	
GER	239	Erodium manescavii Coss.	BG-HEID	HEID	S	1.1	0	0	5	
GER	239	Geranium cinereum Cav.	BG-HEID	HEID	S	1.1	0	0	5	
GER	239	Geranium sanguineum L.	BG-HEID	HEID	S	1.2	0	0	5	
GER	239	Pelargonium tetragonum (L.f.) L'Herit. ex Ait.	BG-HEID	HEID	S	1.6	0	0	8	(1977)
LDC	241	Wendtia gracilix Meyen	Chile, R. Rodriguez & J. Grau 2164	CONC	S	0.9	0	0	3	
BBS	242	Biebersteinia multifida DC.	Armenia, USSR, Gabrielian	HEID	S	1.1	0	0	2	
IXO	248	Ixonanthes grandiflora Hochr.	BG-BO	HEID	S	1.3	0	0	10	
IXO	248	Ixonanthes reticulata Jack.	Sabah, H.D.B. & Lee 830721	HEID	S	1.0	0	0	10	
HOU	246	Endopleura sp.	Brazil, B. Nelson 1566	MO	P5cs	1.2	10	0.3	15	
HOU	246	Humiria balsamifer	Brazil, B. Nelson	HEID	P5cs	1.3	20	0.3	5	
HOU	246	Sacoglottis sp.	Brazil, B. Nelson 1506	MO, HEID	P5sc	0.9	6	0.2	8	
HOU	246	Sacoglottis trichogyna Cuatr.	Costa Rica, M. H. Grayum 7662	MO, HEID	P5cs	1.3	10	0.3	8	
HUG	245 LIN	Hugonia mystax L.	Sri Lanka, Gunatilleke	HEID	S	1.0	0	0	10	
HUG	245 LIN	Indorouchera griffithiana H. Hallier	BG-BO	HEID	S	1.1	0	0	10	
ERX	249	Erythroxylum coca Lam.	BG-HEID	HEID	P5c	1.1	10	0.6	0	(1984)
ERX	249	Erythroxylum novo-granatense (Morris) Hieron	BG-HEID	HEID	P5c	1.3	10	0.5	0	(1984)
ERX	249	Erythroxylum pulchrum A. St. Hil.	BG-RB, Kubitzki		P5c	1.1	10	0.7	0	(1984)

TABLE 1. *Continued.*

Family	D'1989	Species	Origin of Material	Herbarium	Type	DIA	N	PMA	SN	Publication
ERX	249	*Erythroxylum suberosum* A. St. Hil.	Brazil, *I. S. Gottsberger* BG-HEID	BOTU, UB	P5c	1.1	10	0.4	0	(1984)
LIN	245	*Linum dolomiticum* Borb.	BG-HEID		S	1.0	0	0	3	
LIN	245	*Linum flavum* L.	BG-HEID	HEID	S	1.2	0	0	8	
LIN	245	*Reinwardtia cicanoba* (Buch.-Ham. ex D. Don) Hara	BG-K	HEID	S	1.5	0	0	5	
LPB	250	*Lepidobotrys staudtii* Engl.	Cameroon, *D. Thomas & E. Martin 478* BG-HEID	MO, HEID	S	1.2	0	0	10	
OXL	251	*Averrhoa carambola* L.	BG-HEID, -BONN	HEID	Pcfs	1.0	2	0.4	3	(1982c)
OXL	251	*Biophytum sensitivum* (L.) DC.	BG-HEID, -BONN	HEID	S	0.8	0	0	3	(1982c)
OXL	251	*Hypseocharis pimpinellifolia* Remy	BG-CP		S	1.3	0	0	15	(1982c)
OXL	251	*Oxalis acetosella* L.	Heidelberg, *H.D.B. 790413* BG-HEID	HEID	Pc	0.8	2	0.4	0	(1982c)
OXL	251	*Oxalis carnosa* Mol.	BG-HEID	HEID	Pc	0.8	2	0.5	0	(1982c)
OXL	251	*Oxalis crenata* Jacq.	BG-HEID	HEID	Pc	0.8	2	0.5	0	(1982c)
OXL	251	*Oxalis deppei* Lodd. ex Sweet	BG-HEID	HEID	Pc	0.8	2	0.5	0	(1982c)
OXL	251	*Oxalis gigantea* Baun.	BG-SBBG		Pc	1.0	2	0.5	0	(1982c)
OXL	251	*Oxalis rhombifolia* Jacq.	BG-MJG		Pc	0.8	2	0.5	0	(1982c)
OXL	251	*Oxalis stricta* L.	BG-HEID		Pc	0.8	2	0.4	0	(1982c)
OXL	251	*Oxalis valdiviensis* Barbeoud	BG-HEID		Pc	0.9	2	0.5	0	
OXL	251	*Sarcotheca diversifolia* H. Hallier	Sabah, *H.D.B. & Lee 830722* BG-DES	HEID	Pcfs	1.2	2	0.3	5	
CEL	256	*Canotia holacantha* Torr.	BG-HEID	HEID	S	1.1	0	0	5	
CEL	256	*Catha edulis* Forsk.	BG-HEID		S	1.3	0	0	5	
CEL	256	*Celastrus buxifolius* L.	BG-HEID		S	1.3	0	0	10	
CEL	256	*Celastrus orbiculatus* Thunb. var. *punctatus*	BG-HEID	HEID	S	1.4	0	0	5	
CEL	256	*Elaeodendron shaerophyllum* Presl.	BG-K		S	1.1	0	0	5	
CEL	256	*Euonymus fortunei* (Turcz.) Hand.-Mazz.	BG-HEID	HEID	S	1.6	0	0	10	
CEL	256	*Goupia* sp.	Brazil, *B. Nelson* BG-HEID	HEID	S	1.6	0	0	12	
CEL	256	*Hippocratea comosa* Sw.	BG-P		S	1.8	0	0	5	
CEL	256	*Loeseneriella ritchardii* R. Wilczek	BG-P	HEID	S	1.0	0	0	0	
CEL	256	*Peritassa campestris* (Cambess.) A. C. Smith	Brazil, *I. S. Gottsberger* BG-K	BOTU, UB	S	1.4	0	0	10	
CEL	256	*Pterocelastrus tricuspidatus* Walp.	BG-K	HEID	S	1.0	0	0	5	
CEL	256	*Putterlickia pyracantha* Endl.	BG-SBBG		S	1.4	0	0	5	

Table 1. *Continued.*

Family	D'1989	Species	Origin of Material	Herbarium	Type	DIA	N	PMA	SN	Publication
CEL	256	*Salacia uregaensis* R. Wilczek	BG-BONN		S	1.0	0	0	5	
CEL	256	*Siphonodon australis* Benth.	BG-NSW		S	1.1	0	0	10	
ELC	258	*Aceratium dasyphyllum* A. C. Smith	BG-BO	HEID	S	1.2	0	0	5	
ELC	258	*Aristotelia chilensis* (Mol.) Stuntz	BG-BONN	HEID	S	1.4	0	0	5	
ELC	258	*Crinodendron patagua* Mol.	BG-BONN	HEID	S	1.1	0	0	5	
ELC	258	*Elaeocarpus acronodia* Blume	BG-BO	HEID	S	1.7	0	0	10	
ELC	258	*Elaeocarpus ganitrus* Roxb.	Hawaii, Waimea-Arboretum		S	1.6	0	0	10	
RHZ	257	*Bruguiera gymnorrhiza* Lam.	BG-B	GH-B	P5c	1.2	20	0.5	0	(1982a)
RHZ	257	*Bruguiera sexangula* Lour.	BG-CP		P5c	—	20	0.4	0	(1982a)
RHZ	257	*Carallia brachiata* Merrill	QLD, *R. Tracey 281278*		P5c	1.3	20	0.4	0	(1982a)
RHZ	257	*Cassipourea barteri* (Hook. f.) N. E. Br.	BG-BR	HEID	P5c	1.5	20	0.4	0	(1982a)
RHZ	257	*Cassipourea elliptica* (Sw.) Poir.	Costa Rica, *Juncosa 260879*	DUKE, HEID	P5c	1.5	20	0.5	0	(1984)
RHZ	257	*Cassipourea killipii* Cuatrecasas	Columbia, *Juncosa 2540*	JAUM, COL, MO, HEID	P5c	1.2	20	0.4	0	(1984)
RHZ	257	*Ceriops tagal* C. B. Robinson	QLD, *G. J. Muller*	HEID	P5c	1.3	20	0.6	0	(1984)
RHZ	257	*Crossostylis biflora* Forst.	BG-E		P5c	1.3	20	0.3	0	(1982a)
RHZ	257	*Crossostylis grandiflora* Brogn. & Gris.	New Caledonia, *Juncosa 2009814*	DUKE, HEID	P5c	1.3	20	0.3	0	(1984)
RHZ	257	*Kandelia rheedii* Wight & Arn. (= *R. stylosa*)	QLD, *R. Tracey 281278*		P5c	1.4	20	0.3	0	(1982a)
RHZ	257	*Rhizophora cf. conjugata* L.	BG-BONN		P5c	1.5	20	0.3	0	(1982a)
RHZ	257	*Rhizophora mangle* L.	BG-HEID	HEID	P5c	1.4	20	0.3	0	(1982a)
RHZ	257	*Sterigmapetalum heterodoxum* Steyerm. & Liesner	Venezuela, *Berry & Wingfield 4304*	HEID	P5c	1.4	20	0.3	0	(1984)
CUN	163	*Aphanopetalum resinosum* Endl.	BG-K	HEID	S	1.2	0	0	6	
CUN	163	*Caldcluvia paniculata* D. Don.	BG-DUSS		S	1.0	0	0	8	(1985)
CUN	163	*Cunonia capensis* L.	BG-BR	HEID	S	1.3	0	0	10	
CUN	163	*Schizomeria ovata* D. Don	NSW, *H.D.B. 810819*		S	1.2	0	0	0	
CUN	163	*Weinmannia trichosperma* Cav.	BG-DUSS		S	1.1	0	0	5	
BAU	164	*Bauera rubioides* Andr.	NSW, *H.D.B. 810817*, BG-K		S	0.8	0	0	5	
BNL	165	*Brunellia costaricensis* Standley	Costa Rica, *Barringer 2931*	F, CR	S	1.3	0	0	10	
BNL	165	*Brunellia* sp.	Ecuador, *Balslev 62509*		S	1.7	0	0	10	
BNL	165	*Brunellia standleyana* Cuatr.	Costa Rica, *Poveda 3315a*	CR	S	1.2	0	0	10	

TABLE 1. *Continued.*

Family	D'1989	Species	Origin of Material	Herbarium	Type	DIA	N	PMA	SN	Publication
DVS	166	*Davidsonia pruriens* F. Muell.	BG-NSW		S	1.4	0	0	10	
ECR	167	*Eucryphia billardieri* Spach.	BG-K		Pc	0.7	2	0.4	0	(1985)
ECR	167	*Eucryphia cordifolia* Cav.	BG-DUSS	HEID	Pc	0.6	2	0.3	0	(1985)
ECR	167	*Eucryphia glutinosa* (Poepp. et Endl.) Baill.	BG-DUSS	HEID	Pc	0.6	2	0.2	0	(1985)
ECR	167	*Eucryphia lucida* Druce	BG-K		Pc	0.6	2	—	0	(1985)
ECR	167	*Eucryphia ×nymansensis* Bausch.	BG-K	HEID	Pc	0.6	2	0.3	0	
CRO	185	*Crossosoma bigelovii* S. Wats.	*A. C. Gibson*, BG-RSA	RSA	S	1.7	0	0	10	
CRO	185	*Crossosoma californicum* Nutt.	BG-RSA, -SBBG	RSA	S	1.8	0	0	10	
CRO	185	*Forsellesia nevadensis* (Gray) Greene	Arizona, *A. C. Gibson*		S	1.0	0	0	0	
ROS	180	*Alchemilla xanthochlora* Rothm.	BG-HEID	HEID	S	0.9	0	0	5	
ROS	180	*Dryas suedermannii* Süderm.	BG-HEID	HEID	So	0.8	0	0	0	
ROS	180	*Duchesnea indica* (Andr.) Focke	BG-HEID	HEID	So	0.9	0	0	0	
ROS	180	*Filipendula ulmaria* (L.) Maxim.	BG-CP		So	0.8	0	0	0	
ROS	180	*Fragaria vesca* L.	BG-HEID	HEID	S	0.9	0	0	1	
ROS	180	*Geum rivale* L.	BG-HEID	HEID	So	0.6	0	0	0	
ROS	180	*Kerria japonica* (L.) DC.	Heidelberg, *H.D.B. 780821*	HEID	S	1.4	0	0	5	
ROS	180	*Lyonothamnus floribundus* A. Gray	BG-SBBG		S	1.6	0	0	10	
ROS	180	*Neviusia alabamensis* A. Gray	BG-BONN	HEID	S	1.3	0	0	5	
ROS	180	*Potentilla rupestris* L.	BG-HEID	HEID	So	0.8	0	0	0	
ROS	180	*Quillaja brasiliensis* Mart.	BG-HEID	HEID	So	1.1	0	0	0	
ROS	180	*Rhodotypus scandens* (Thunb.) Mak.	BG-HEID	HEID	S	1.2	0	0	10	
ROS	180	*Rosa* sp.	BG-HEID	HEID	So	1.0	0	0	0	
ROS	180	*Rubus phoenicolasius* Maxim.	BG-BONN	HEID	So	1.1	0	0	0	
ROS	180	*Sanguisorba minor* Scop.	BG-HEID	HEID	So	0.9	0	0	0	
ROS	180	*Spiraea wilsonii* Duthie	BG-HEID	HEID	S	1.0	0	0	5	
NRD	181	*Neurada procumbens* L.	Kuwait, *L. Boulos*	HEID	Pcs	1.5	1	0.4	10	
ANS	184	*Anisophyllea cf. purpurascens* Hutchins. & Dalz.	Cameroon, *D. Thomas 6120*	MO	S	1.2	0	0	10	
ANS	184	*Anisophyllea trapezoidales* Baill.	Sabah, *H.D.B 830721*	HEID	S	1.2	0	0	10	(1984)[1]
ANS	184	*Combretocarpus cf. motleyi* Hook. f.	Sarawak, *Sri Aman*		S	1.1	0	0	10	(1984)
ANS	184	*Poga oleosa* Schott	Cameroon, *D. Thomas 6119*	MO	S	1.3	0	0	10	
ANS	184	*Polygonanthus amazonicus* Ducke	Brazil, *B. Nelson*	MO	S	1.4	0	0	10	

TABLE 1. *Continued.*

Family	D'1989	Species	Origin of Material	Herbarium	Type	DIA	N	PMA	SN	Publication
MAL	182	*Amelanchier canadensis* (L.) Medik.	BG-HEID		S	1.0	0	0	5	
MAL	182	*Aronia prunifolia* (Marsh.) Rehder	BG-HEID	HEID	S	1.2	0	0	5	
MAL	182	*Cotoneaster frigidus* Wall. ex Lindl.	BG-HEID		S	1.2	0	0	5	
MAL	182	*Crataegus ×dippeliana* Lange	BG-HEID	HEID	S	1.4	0	0	5	
MAL	182	*Cydonia oblonga* Mill.	BG-HEID	HEID	S	1.3	0	0	5	
MAL	182	*Eriobotrya japonica* (Thunb.) Lindl.	BG-HEID		S	1.2	0	0	10	
MAL	182	*Malus sylvestris* Mill.	BG-HEID		S	1.6	0	0	10	
MAL	182	*Mespilus germanica* L.	BG-SIENA		S	1.0	0	0	5	
MAL	182	*Pyracantha coccinea* M. J. Roem.	Heidelberg, *H.D.B. 780821*	HEID	S	1.4	0	0	10	
MAL	182	*Pyrus communis* L.	Heidelberg, *H.D.B. 780821*		S	1.0	0	0	10	
MAL	182	*Raphiolepis indica* Lindl.	BG-HEID		S	1.0	0	0	10	
MAL	182	*Sorbus aucuparia* L.	BG-HEID	HEID	S	1.2	0	0	10	
MAL	182	*Vauquelinia californica* Sarg.	BG-SBBG		S	1.2	0	0	10	
AMY	183	*Exochorda giraldii* Hesse	BG-HEID	HEID	S	0.9	0	0	3	
AMY	183	*Prunus cerasifera* Ehrh.	BG-HEID	HEID	S	1.2	0	0	0	
AMY	183	*Prunus padus* L.	BG-HEID	HEID	S	1.0	0	0	5	
AMY	183	*Prunus scoparius* Schneider	BG-HEID	HEID	S	0.9	0	0	10	
RHB	187	*Rhabdodendron amazonicuum* (Spruce ex Benth.) Hub.	Brazil, *G. T. Prance s.n.*	NY	Pcs	1.0	1	0.3	5	(1976a)
RHB	187	*Rhabdodendron macrophyllum* (Spruce ex Benth.) Hub.	Brazil, *G. T. Prance 20187; and B. Nelson 1290*	MO, HEID	Pcs	1.4	1	0.2	5	(1976a)
SAX	168	*Astilbe simplicifolia* Mak.	BG-HEID	HEID	S	1.2	0	0	8	
SAX	168	*Bergenia purpurascens* (Hook. f. & Thoms.) Engl.	BG-HEID	HEID	S	1.2	0	0	5	
SAX	168	*Peltiphyllum peltatum* (Torr.) Engl.	BG-CP		S	1.6	0	0	10	
SAX	168	*Rodgersia aesculifolia* Batal	BG-BONN	HEID	S	1.4	0	0	8	
SAX	168	*Saxifraga paniculata* Mill.	BG-HEID	HEID	S	1.0	0	0	8	
SAX	168	*Tolmiea menziesii* (Pursch.) Torr. et A. Gray	BG-HEID	HEID	S	1.3	0	0	10	
PTH	168 SAX	*Penthorum sedoides* L.	N. Carolina, *A. E. Radford* and BG-HAM	NCU	S	1.2	0	0	8	
VHL	168 SAX	*Vahlia capensis* Thunb.	BG-PRE	HEID	S	1.2	0	0	10	
FCO	169	*Francoa sonchifolia* Cav.	BG-BONN, -K	HEID	S	1.4	0	0	3	
GRY	170	*Greyia sutherlandii* Hook. et Harv.	BG-BONN, -HEID	HEID	S	1.2	0	0	5	

TABLE 1. *Continued.*

Family	D'1989	Species	Origin of Material	Herbarium	Type	DIA	N PMA	SN	Publica- tion
BRX	171	*Brexia madagascariensis* (Lam.) Nor. ex Thou.	BG-K, -BERN		S	1.1	0	5	
GRS	172	*Ribes bracteosum* Dougl. ex Hook.	BG-HEID		S	1.2	0	10	
ITE	173	*Choristylis rhamnoides* Harv.	BG-K		S	1.3	0	5	
ITE	173	*Itea ilicifolia* Oliv.	BG-K	HEID	S	1.6	0	5	
CPH	174	*Cephalotus follicularis* Labill.	BG-M		S	1.1	0	5	
CRS	175	*Cotyledon orbiculatum* L.	BG-HEID	HEID	So	1.0	0	0	
CRS	175	*Kalanchoe laciniata* (L.) DC.	BG-HEID	HEID	So	0.9	0	0	
CRS	175	*Kalanchoe uniflora* (Stapf) R. Ha- met.	BG-HEID	HEID	So	0.8	0	0	
PDS	176	*Podostemum ceratophyllum* Michx.	Georgia, S. B. Jones; and D. E. Boufford 22047	CM	S	2.3	0	8	

¹ Erroneously listed in Table 1 of Behnke (1984) as PVc.

Celastraceae (CEL; Fig. 4: *Catha*, *Pterocelastrus*). Fourteen species in 13 genera investigated, all with S-type plastids. There are 5–10 mostly globular starch grains recorded within these plastids, but their diameter is not uniform (average: 1.3 μm; range 1.0–1.8 μm). The sieve elements of *Goupia* contain crystalline, persistent p-protein bodies, a feature that characterizes a number of different dicotyledonous taxa (see Behnke, 1981) but is not found elsewhere in Celastraceae. *Hippocratea* and *Salacia*, as well as *Siphonodon*, sometimes separated as Hippocrateaceae and Siphonodontaceae, respectively, do not differ significantly in sieve-element characters.

Elaeocarpaceae (ELC; Fig. 4: *Aristotelia*, *Elaeocarpus*). The five species in four genera investigated contain S-type plastids. Their sizes (1.1–1.7 μm; average 1.4 μm) and number of globular starch grains (5–10) resemble those in CEL.

Rhizophoraceae (RHZ; Fig. 5: *Cassipourea*, *Ceriops*, *Crossostylis*, *Rhizophora*, *Sterigmapetalum*). Thirteen species of eight genera investigated, all with the specific form-P5c sieve-element plastids. Twenty or more rectangular to irregular protein crystals (0.2–0.5 μm) fill the plastid interior. The average plastid diameter is 1.4 μm. In *Rhizophora* the protein crystals are irregular, only rarely showing exact rectangular outlines. It is demonstrated, at least for *R. mangle*, that during the development of a sieve-element plastid, protein accumulates first as a large granular body (see Fig. 5, lower left micrograph) and only thereafter 'crystallizes' into several distinct parts.

In this study of their sieve-element plastids, all of the tribes recognized within the family were covered. Except for the crystal outlines mentioned for *Rhizophora*, there is almost no distinction possible between the plastids of the different species. The comparatively large protein crystals depicted in *Ceriops* (Fig. 5), which come very close in size to those shown in *Erythroxylum* (Fig. 2), are not restricted to this species. Similar views could have been chosen from other Rhizophoraceae. (See also Behnke, 1982a, 1984.)

DISTRIBUTION OF THE DIFFERENT SIEVE-ELEMENT PLASTIDS AMONG THE FAMILIES GROUPED AROUND ANISOPHYLLEACEAE

Cunoniaceae (CUN; Fig. 6: *Cunonia*, *Weinmannia*). Five species of five genera investigated, all with S-type plastids. The diameter of the plastids is about 1.2 μm; their contents are up to

TABLE 2. *The families of the ordinal periphery around Anisophylleaceae and Rhizophoraceae arranged according to sieve-element plastid data.*

Family	Types	PSP[1]	PDIA	N	PMA	PS	SSP	SDIA	SN	SO	SODI	Dahlgren
Brunelliaceae	S						3	1.4	10			BNL 165
Davidsoniaceae	S						1	1.4	10			DVS 166
Cunoniaceae	S						5	1.2	7			CUN 163
Baueraceae	S						1	0.8	5			BAU 164
Eucryphiaceae	Pc	5	0.6	2	0.3							ECR 167
Saxifragaceae	S						6	1.3	8			SAX 168
Penthoraceae	S						1	1.2	8			PTH 168
Vahliaceae	S						1	1.2	10			VHL 168
Francoaceae	S						1	1.4	3			FCO 169
Greyiaceae	S						1	1.2	5			GRY 170
Brexiaceae	S						1	1.1	5			BRX 171
Grossulariaceae	S						1	1.2	10			GRS 172
Iteaceae	S						2	1.4	5			ITE 173
Cephalotaceae	S						1	1.1	5			CPH 174
Crassulaceae	So									3	0.9	CRS 175
Crossosomataceae	S						3	1.5	10			CRO 185
Anisophylleaceae	S						5	1.2	10			ANS 184
Rosaceae	S, So						7	1.2	6	9	0.9	ROS 180
Malaceae	S						13	1.2	8			MAL 182
Amygdalaceae							4	1.0	6			AMY 183
Rhabdodendraceae	Pcs	2	1.2	1	0.3	5						RHB 187
Neuradaceae	Pc	1	1.5	1	0.4	10						NRD 181
Gunneraceae	Pc	3	1.5	2	0.5	8						GNN 188
Podostemaceae	S						1	2.3	8			PDS 176
Balanitaceae	S						2	1.4	10			BLT 244
Zygophyllaceae	S, Pcs	1	1.1	2	0.4	5	4	1.3	7			ZYG 236
Nitrariaceae	S						1	1.0	6			NIT 238
Peganaceae	S						1	1.2	5			PEG 237
Geraniaceae	S						5	1.2	6			GER 239
Vivianiaceae	S						1	1.1	5			VIV 240
Ledocarpaceae	S						1	0.9	3			LDC 241
Biebersteiniaceae	S						1	1.1	2			BBS 242
Linaceae	S						3	1.2	7			LIN 245
Hugoniaceae	S						2	1.1	10			HUG 245
Ixonanthaceae	S						2	1.2	10			IXO 248

TABLE 2. Continued.

Family	Types	PSP¹	PDIA	N	PMA	PS	SSP	SDIA	SN	SO	SODI	Dahlgren
Lepidobotryaceae	S											LPB 250
Hypseocharitaceae	S											OXL 251
Oxalidaceae	S, Pc	8	0.8	2	0.5	4	1	1.2	10			OXL 251
Averrhoaceae	Pcfs	2	1.1	2	0.4	4	1	1.3	15			OXL 251
Humiriaceae	P5cs	4	1.2	12	0.3	9	1	0.8	3			HOU 246
Erythroxylaceae	P5c	4	1.2	10	0.6							ERX 249
Rhizophoraceae	P5c	13	1.4	20	0.4							RHZ 257
Celastraceae	S						14	1.3	7			CEL 256
Elaeocarpaceae	S						5	1.4	7			ELC 258
Cyrillaceae	P5cf	2	1.6	9	0.8							CYR 297

¹ PSP = number of P-type species; PDIA = average diameter of P-type plastids; N = average number of protein crystals; PS = average number of starch grains in P-type plastids; SSP = number of S-type species; SDIA = average diameter of S-type species; SN = average number of starch grains in S-type plastids; SO = number of form-So plastids; SODI = average diameter of form-So plastids; Dahlgren = family acronym and position of family in Dahlgren (in press).

10 globular starch grains, often surrounded by additional tiny granules. (See also Behnke, 1985.)

Baueraceae (BAU; Fig. 6: *Bauera*). *Bauera rubioides* as representative of the monogeneric family contains very small (diameter 0.8 μm) S-type plastids with up to five small irregular starch grains.

Brunelliaceae (BNL; Fig. 6: *Brunellia*). The three species of *Brunellia* investigated contain S-type plastids. Their globular starch grains (about 10 in the average) often seem to disintegrate into tiny pieces. The plastid diameter is 1.4 μm.

Davidsoniaceae (DVS; Fig. 6: *Davidsonia*). The monotypic *Davidsonia pruriens* contains S-type plastids with about 10 strictly globular starch grains. The plastid diameter is 1.4 μm.

Eucryphiaceae (ECR; Fig. 6: *Eucryphia*). Four of the five species of this monogeneric family and one hybrid were found to contain form-Pc sieve-element plastids with two protein crystals, one with a diameter of about 0.3 μm. The sieve-element plastids of *Eucryphia* are among the tiniest recorded within the dicotyledons (average diameter of 0.6 μm). (See also Behnke, 1985.)

Crossosomataceae (CRO; Fig. 8: *Crossosoma*). Three species in two genera investigated, all with S-type plastids. The two *Crossosoma* species are identical, both in respect to their plastid diameter (1.8 μm) and the starch content (about 10 globular grains). *Forsellesia* has smaller plastids (diameter 1.0 μm) and fewer starch grains.

Rosaceae (ROS; Fig. 7: *Duchesnea*). Sixteen species in 16 genera investigated; all species with S-type plastids, but nine of them without starch (with form-So plastids). The average diameter of the plastids is 1.0 μm, with an average of 0.9 μm for the So form and of 1.2 μm for those with starch grains. The average number of grains in the starch-containing species is six.

Neuradaceae (NRD; Fig. 8: *Neurada*). *Neurada procumbens* contains form-Pcs sieve-element plastids with one rectangular protein crystal (diameter 0.4 μm) and up to five large starch grains. The diameter of the plastids is 1.5 μm. With these characteristics, there is resemblance to the sieve-element plastids of *Gunnera*. (See Behnke, 1986b.)

Anisophylleaceae (ANS; Fig. 8: *Anisophyllea, Combretocarpus, Poga, Polygonanthus*). Five species in four genera investigated; all have S-type plastids. With diameters of about 1.2 μm and some ten globular starch grains, the sieve-element plas-
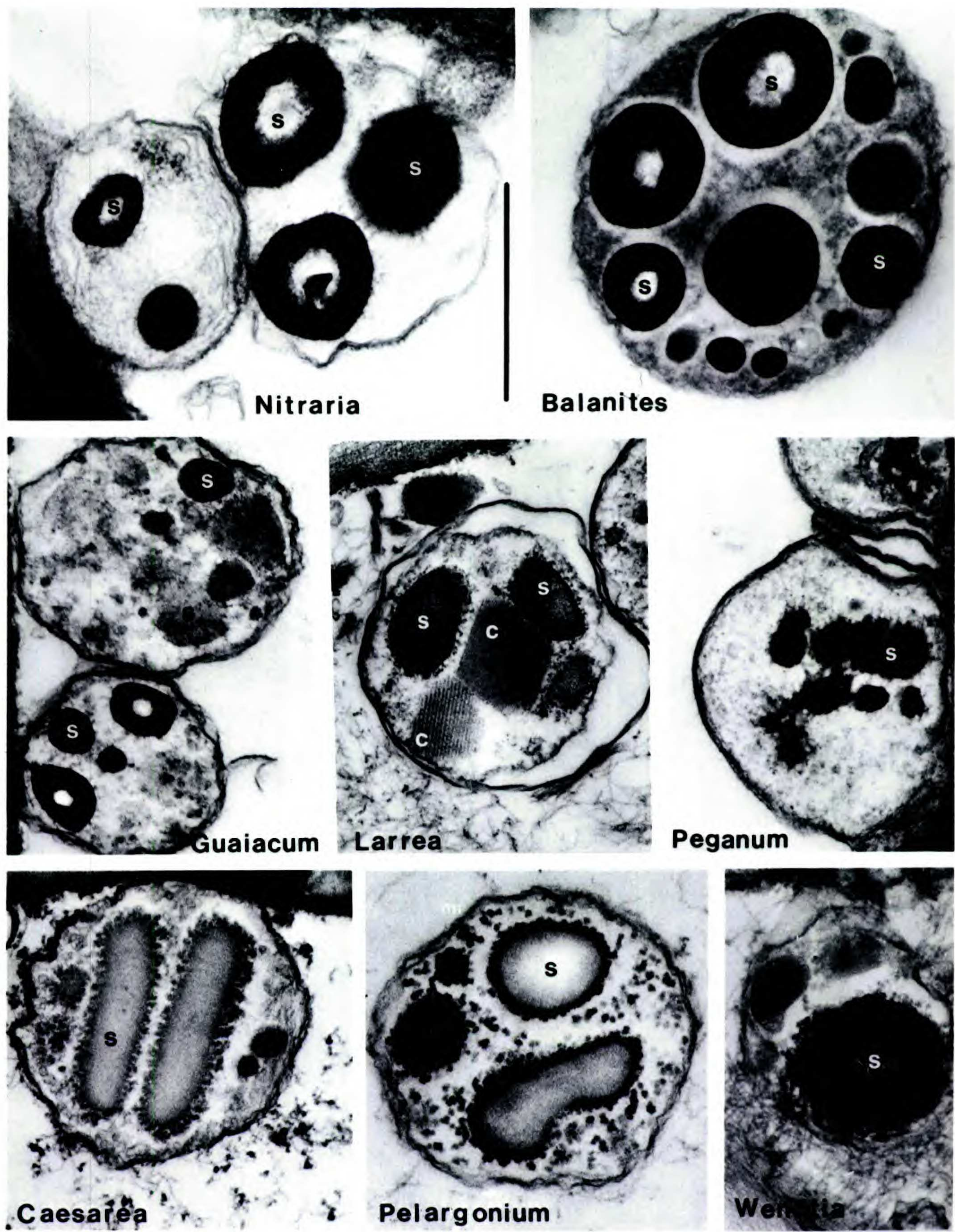
FIGURE 1. *S-type sieve-element plastids of* Nitraria retusa, Balanites aegyptiaca, Guaiacum coulteri, Peganum harmala, Caesarea albiflora, Pelargonium tetragonum, *and* Wendtia gracilis; *and P-type plastids of* Larrea divaricata. *All* ×30,000. *c = protein crystals, s = starch grains. Scale bar = 1 µm.*
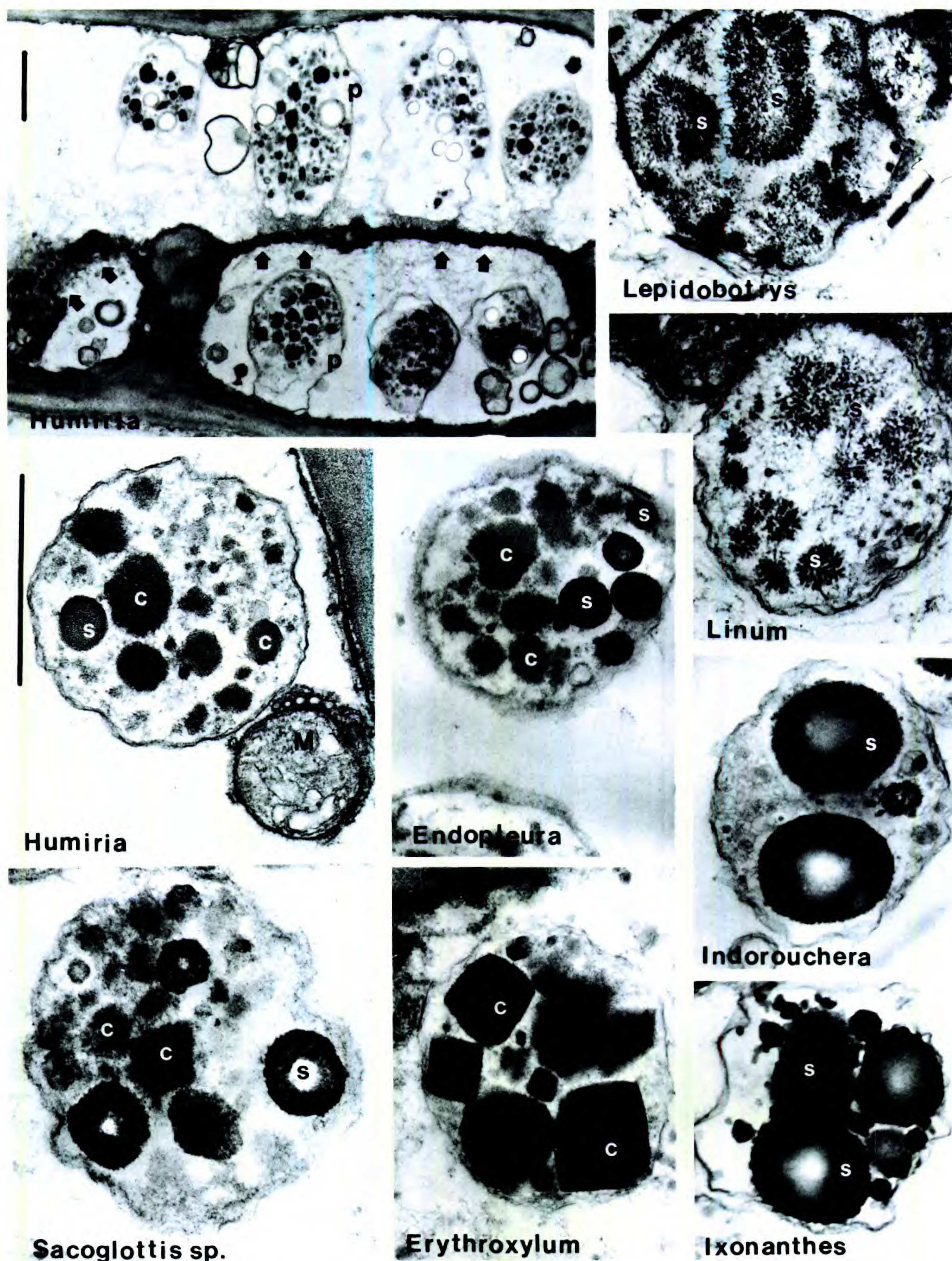
FIGURE 2. *Upper left: longitudinal section through sieve elements of* Humiria balsamifer *with compound sieve plate (arrows) and several P-type sieve-element plastids (p)*, ×10,000. *Other photographs: sieve-element plastids of* Lepidobotrys staudtii, Linum flavum, Indorouchera griffithiana, Ixonanthes grandiflora; *and P-type plastids of* Humiria balsamifer, Endopleura *sp.,* Sacoglottis *sp., and* Erythroxylum coca. *All* ×30,000. *c* = *protein crystals, s* = *starch grains, M* = *mitochondrion. Scale bars* = *1 μm.*
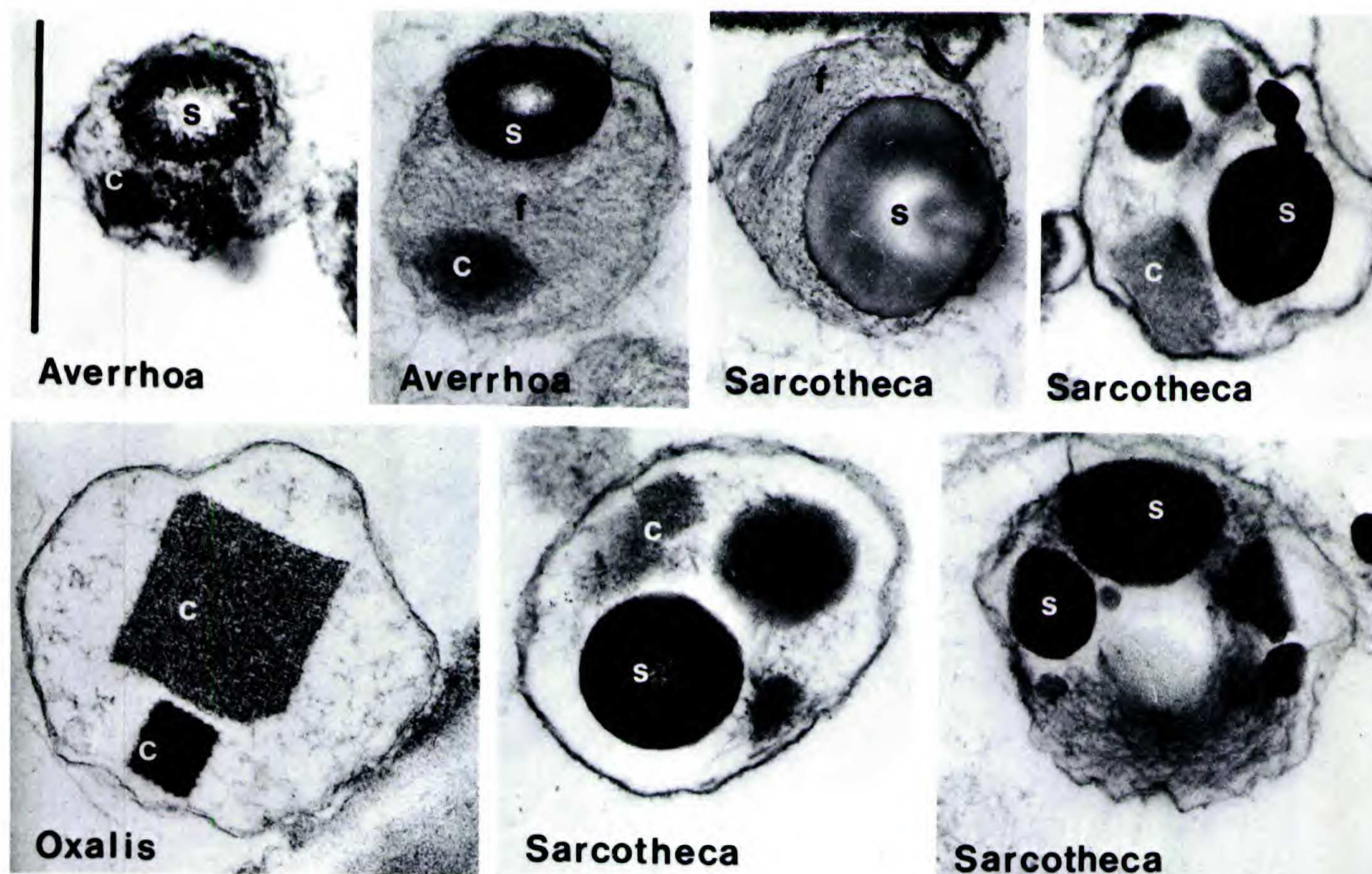
FIGURE 3. *P-type sieve-element plastids of* Averrhoa carambola, Sarcotheca diversifolia, *and* Oxalis deppei. *All* ×30,000. c = *protein crystals, f = protein filaments, s = starch grains. Scale bar = 1 μm.*

tids of the Anisophylleaceae are rather homogeneous and very distinct from those of the Rhizophoraceae. The difference in the plastid types supports elevation of the former tribe Anisophylleeae to family status. (See also Behnke, 1984.)

Malaceae (MAL; Fig. 7: *Amelanchier*). Thirteen species in 13 genera investigated; all have S-type plastids. The average diameter of the plastids is 1.2 μm, and the average number of starch grains eight. These data do not differ from those of the S-type Rosaceae. No form-So plastids are found in the Malaceae.

Amygdalaceae (AMY; Fig. 7: *Prunus*). Four species in two genera investigated, all with S-type plastids. The plastids in this family are smaller (average diameter 1.0 μm) than those in ROS and MAL, although their starch content is similar.

Rhabdodendraceae (RHB; Fig. 8: *Rhabdodendron*). The two species investigated of this monogeneric family contain form-Psc sieve-element plastids. Their single protein crystal is rectangular and about 0.2 μm in diameter. There are about five irregular starch grains. The average plastid diameter is 1.2 μm. (See also Behnke, 1976a.)

Saxifragaceae (SAX; Fig. 7: *Bergenia*). Six species in six genera investigated, all with S-type plastids. The average plastid diameter is 1.3 μm;

there are about eight irregularly shaped starch grains in the plastids.

Penthoraceae (PTH; Fig. 7: *Penthorum*). *Penthorum sedoides* as representative of the monogeneric family contains S-type plastids with characters almost identical to those in SAX, i.e., with a diameter of 1.2 μm and containing about eight starch grains.

Vahliaceae (VHL; Fig. 7: *Vahlia*). The S-type plastids recorded for *Vahlia capensis* show the same pattern as found in SAX—diameter 1.2 μm and containing about ten starch grains.

Francoaceae (FCO; Fig. 7: *Francoa*). The investigated *Francoa sonchifolia* contains S-type plastids only slightly different from those in SAX; their diameter is 1.4 μm; the number of starch grains is about three.

Greyiaceae (GRY; Fig. 7: *Greyia*). *Greyia sutherlandii* contains S-type plastids with about five globular starch granis. The plastid diameter is 1.2 μm.

Brexiaceae (BRX; Fig. 7: *Brexia*). *Brexia madagascariensis* was shown to contain S-type plastids about 1.1 μm in diameter with about five starch grains.

Grossulariaceae (GRS; Fig. 7: *Ribes*). *Ribes*

bracteosum contains S-type plastids with about ten globular starch grains and a diameter of 1.2 μm.

Iteaceae (ITE; Fig. 7: *Itea*). Two species in the two genera investigated; both contain S-type plastids with about five starch grains that disintegrate into tiny particles. The average plastid diameter is 1.5 μm.

Cephalotaceae (CPH; Fig. 7: *Cephalotus*). The monotypic *Cephalotus follicularis* contains S-type plastids with about five starch grains and a diameter of 1.1 μm. The starch grains are slightly disc-shaped and surrounded by tiny particles.

Crassulaceae (CRS; Fig. 7: *Cotyledon*). Three species in two genera shown to contain form-So sieve-element plastids. Their average diameter is 0.9 μm. Many more species were investigated, but although the fixation of the material was satisfactory, repeated screening failed to detect sieve-element plastids. Most likely, the So-plastids easily break down during the differentiation of the sieve elements. Similar conclusions were made from studies with *Cucurbita* species that also contain form-So plastids (Buvat, 1963; Esau & Cronshaw, 1968).

In Crassulaceae the form-So plastids sometimes contain small inclusions, which rarely show a crystalline composition. Since they are probably related to protein crystals, sieve-element plastids of CRS were also defined as Po/So. (See Behnke, 1981.)

Podostemaceae (PDS; Fig. 7: *Podostemum*). *Podostemum ceratophyllum* contains S-type plastids with about eight starch grains, often surrounded by tiny particles. The diameter of the plastids is 2.3 μm, by far the highest found among the taxa studied for this report.

DISCUSSION

The results from investigations of the sieve-element plastids reported here unambiguously support separation of the tribe Aniosphylleeae from the Rhizophoraceae and its elevation to the rank of a family. The very distinct and remarkable form-P5c sieve-element plastids of Rhizophoraceae s. str.— without any incorporation of even traces of starch— has no direct relationhip to the pure S-type (lacking any amount of protein) as found in the Anisophylleaceae. According to a model demonstrating the interrelationships between the different forms of sieve-element plastids (proposed by Behnke, 1988), at least two evolutionary steps would be necessary to change the S-type into a form-Pc sieve-element plastid. Without the presence of in-
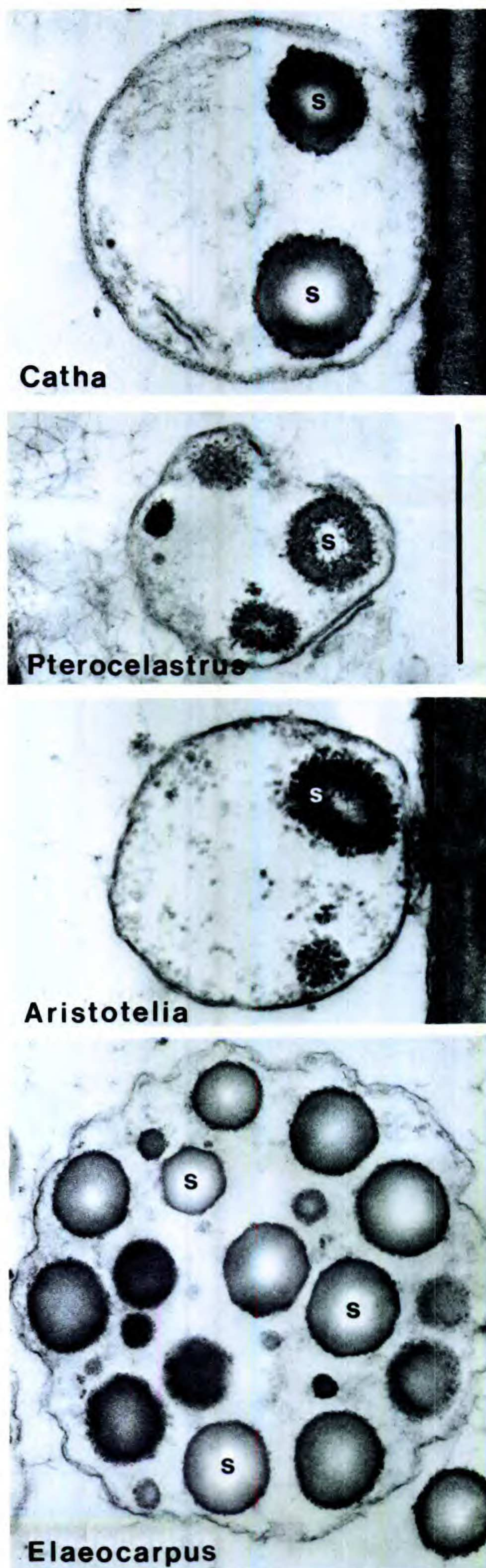
FIGURE 4. *S-type sieve-element plastids of* Catha edulis, Pterocelastrus tricuspidatus, Aristotelia chilensis, *and* Elaeocarpus ganitrus. *All* ×30,000. *s = starch grains. Scale bar = 1 μm.*
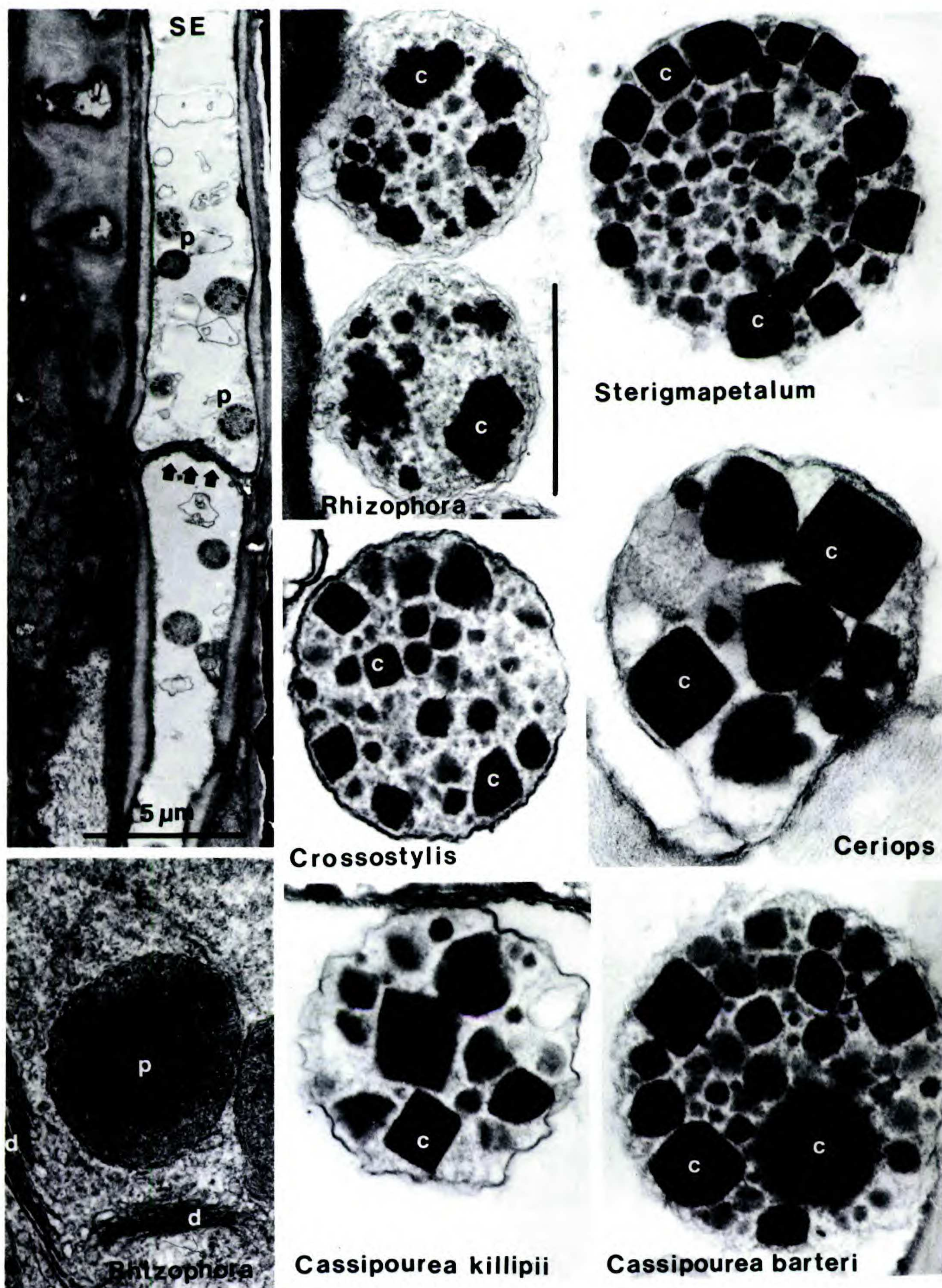
FIGURE 5. *P-type sieve-element plastids of the Rhizophoraceae. Upper left: longitudinal section through primary phloem of* Rhizophora mangle *showing two members of a sieve tube (SE) connected by a sieve plate (arrows) and containing several P-type plastids (p);* ×5,000. *Lower left: P-type plastids of a young sieve element of* R. mangle. *Plastid matrix filled with granular protein material (p), not yet differentiated into crystals; d = dictyosomes;* ×30,000. *Other photographs, from top to bottom: P-type plastids of* R. mangle, Sterigmapetalum heterodoxum, Crossostylis grandiflora, Ceriops tagal, Cassipourea killipii, *and* Cassipourea barteri. *All* ×30,000. *c = protein crystals. Scale bar = 1 μm.*
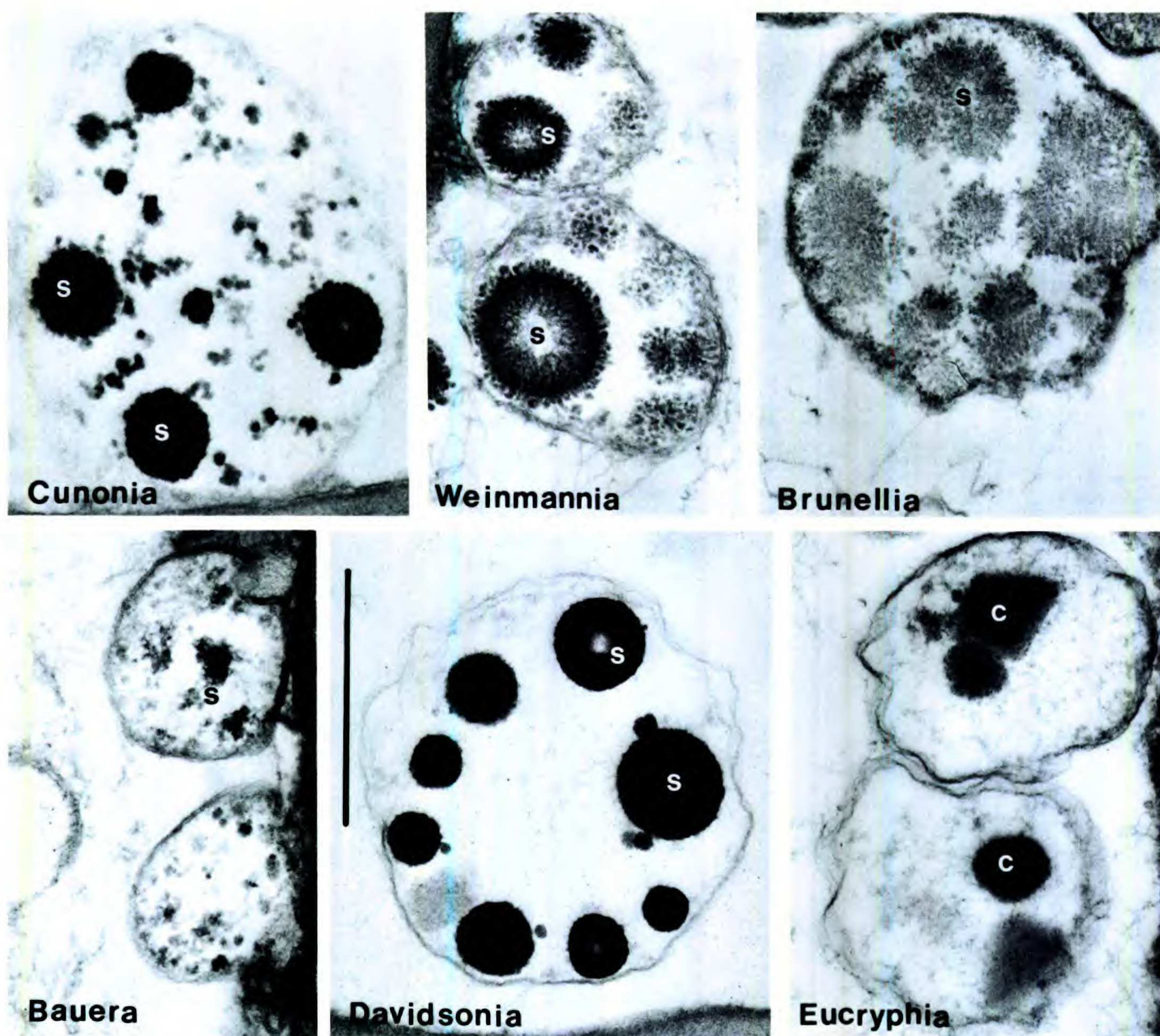
FIGURE 6. *S-type sieve-element plastids of* Cunonia capensis, Weinmannia trichosperma, Brunellia *sp.*, Bauera rubioides, Davidsonia pruriens, *and form-Pc sieve-element plastids of* Eucryphia billardieri. *All* ×30,000. c = protein crystals, s = starch grains. Scale bar = 1 μm.

termediates the coexistence of both types within one family is not very likely.

While sieve-element plastids help discriminate between Rhizophoraceae and Anisophylleaceae, determination of their affiliations to other taxa is possible only to a limited extent. Therefore, the position of the two families relative to the taxa proposed by Dahlgren (this volume) to constitute the ordinal periphery will now be discussed.

GERANIALES SENSU LATO

In his last version of the system of classification of dicotyledons, Dahlgren (in press) divided the Geraniales s.l. into two orders, the Geraniales s. str. and the Linales. The following discussion makes use of this separation.

1. (= Geraniales s. str.). Dahlgren (in press) listed Zygophyllaceae, Peganaceae, Nitrariaceae,

Geraniaceae, Vivianiaceae, Ledocarpaceae, Biebersteiniaceae, Dirachmaceae, and Balanitaceae in this alliance. Among the families available for our studies (see Table 2) S-type sieve-element plastids are most common and P-type plastids are found only in *Larrea* (Zygophyllaceae). The diameter of the plastids is rather uniform, varying around 1.1 μm. Some families contain disc-shaped starch grains as a specific marker: Geraniaceae, Vivianiaceae, and Zygophyllaceae (in part).

The S-type plastids of Balanitaceae diverge more from the above pattern (see also Fig. 1). Both Cronquist (1981) and Thorne (1983) placed *Balanites* within Zygophyllaceae; Takhtajan (1987) transferred to Rutales the Zygophyllaceae and those families that, like Balanitaceae, Nitrariaceae, and Peganaceae, were split off earlier. Neither of these assignments is strongly supported by the plastid data.

Amelanchier

Prunus

Duchesnea

Cotyledon

Bergenia

Penthorum

Vahlia

Francoa

Greyia

Ribes

Brexia

Cephalotus

Itea

Podostemon
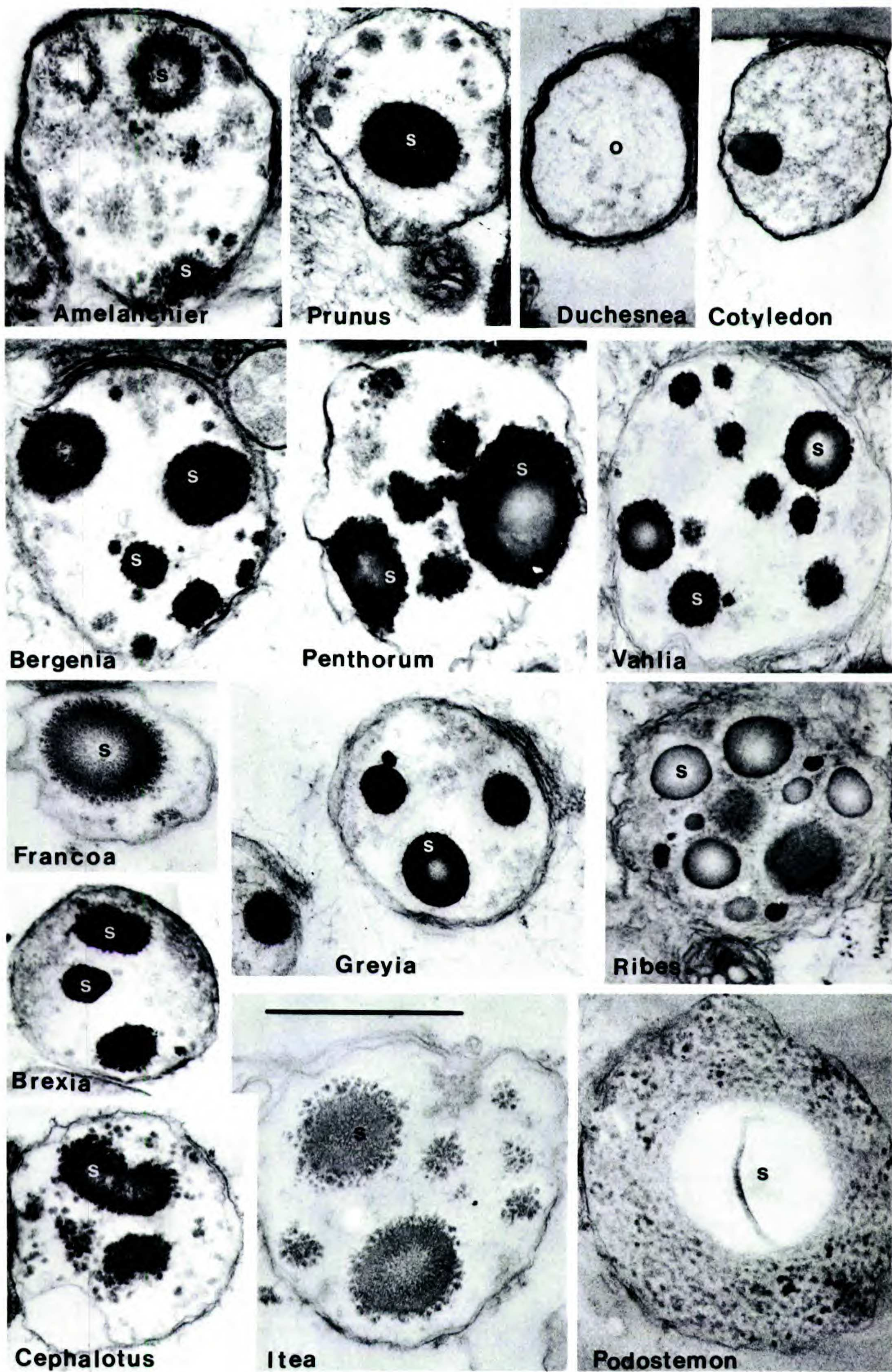
2. (= Linales). Dahlgren (in press), included Linaceae, Hugoniaceae, Humiriaceae, Ctenolophonaceae, Ixonanthaceae, Erythroxylaceae, Lepidobotryaceae, and Oxalidaceae in the Linales. With four S-type families, two P-type families, and one family containing both S-type and two different forms of P-type sieve-element plastids, this suborder is very heterogeneous (fresh material from *Ctenolophon* was not available).

The S-type plastids (in Linaceae, Hugoniaceae, Ixonanthaceae, Lepidobotryaceae, Biebersteiniaceae, and Oxalidaceae) are rather small: their average diameter is about 1.1 μm. From five to ten starch grains, often disintegrating into small particles and sometimes including a very large one, are found within these plastids (see Figs. 2, 3; Behnke, 1982c); a few species differ slightly from this pattern, e.g., in *Reinwardtia* (Linaceae) (Table 1).

The two different forms of P-type plastids recorded within the Oxalidaceae are restricted to different genera: *Averrhoa* and *Sarcotheca* contain form-Pcfs, while *Oxalis* has highly specialized and very small form-Pc sieve-element plastids. Diameters and compositions of these two forms are so different (see Table 1) that it seems justified from the plastid data to support the separation of the families Averrhoaceae (see Hutchinson, 1959) and Hypseocharitaceae (see Takhtajan, 1987).

The two remaining P-type families, Humiriaceae and Erythroxylaceae, contain P-forms not directly related to those of the Oxalidaceae. The form-P5cs plastids found in Humiriaceae are similar to the P4cs plastids of Fabales (cf. Fig. 2 with Behnke & Pop, 1981, figs. 5–15) and can be regarded as transitional between S-type and form-P5c plastids of the Erythroxylaceae. The latter are extraordinarily distinct from all other sieve-element plastids, and the only other family reported to contain this form is the Rhizophoraceae.

Cronquist (1981), Thorne (1983), and Takhtajan (1987) incorporated the Oxalidaceae and Lepidobotryaceae in the Geraniales s. str. Their Geraniales (Geraniineae of Thorne, 1983) differ from each other only slightly. The patterns of the S-type plastids in the Linales and Geraniales are not sufficiently different to favor one or other treatment—and the plastids of *Lepidobotrys*, *Biophytum*, and *Hypseocharis* are intermediate.

Therefore, in the familial sequence given in Ta-

ble 2, which is arranged according to the data obtained with the sieve-element plastids, the order Geraniales s.l. is maintained.

CELASTRALES

Celastraceae and Elaeocarpaceae contain S-type sieve-element plastids to some extent alike in pattern but not very specialized. The families are not very uniform in their sieve-element plastids (e.g., see Fig. 4: *Aristotelia* and *Elaeocarpus*).

Rhizophoraceae contain form-P5c plastids, a highly specialized pattern that is found throughout all genera investigated. In addition, variation in the diameter of the plastids is very small. There seem to be no common sieve-element plastid characters between the Rhizophoraceae and the other two families of this order; the closest similarities are with plastids of Erythroxylaceae.

Thorne (1983) placed Rhizophoraceae in his Cornales; Cronquist (1981) and Takhtajan (1987) regarded their order Rhizophorales as a close ally of the Myrtales. Dahlgren in his last version (in press) put Rhizophoraceae together with Elaeocarpaceae into his order Rhizophorales and gave it a position after Geraniales/Linales and his newly defined Celastrales (including S-type families only).

Sieve-element plastid data suggest a close association of Rhizophoraceae with Humiriaceae and Erythroxylaceae (see Table 2).

CUNONIALES

The S-type sieve-element plastids present in four of the five families of this order are heterogeneous. Plastid diameter and starch content range from large with ten grains to very small with little starch (see Table 1). The sequence given in Table 2 suggests an evolution from the large unspecialized to the small specialized plastid and enables a connection to the only P-type family (Eucryphiaceae).

Exactly the same five families constitute Takhtajan's (1987) Cunoniales. Thorne (1983) added Staphyleaceae and Corynocarpaceae to his suborder Cunoniinae, while Cronquist distributed them among his Rosales.

SAXIFRAGALES

All families within this order contain S-type sieve-element plastids, of which Crassulaceae is special-

FIGURE 7. *S-type sieve-element plastids of* Amelanchier canadensis, Prunus padus, Duchesnea indica *(form-So)*, Cotyledon orbiculatum *(form-So)*, Bergenia purpurascens, Penthorum sedoides, Vahlia capensis, Francoa sonchifolia, Greyia sutherlandii, Ribes bracteosum, Brexia madagascariensis, Cephalotus follicularis, Itea ilicifolia, *and* Podostemum ceratophyllum. *All* × 30,000. s = *starch grains,* o = *form-So plastid. Scale bar = 1 μm.*
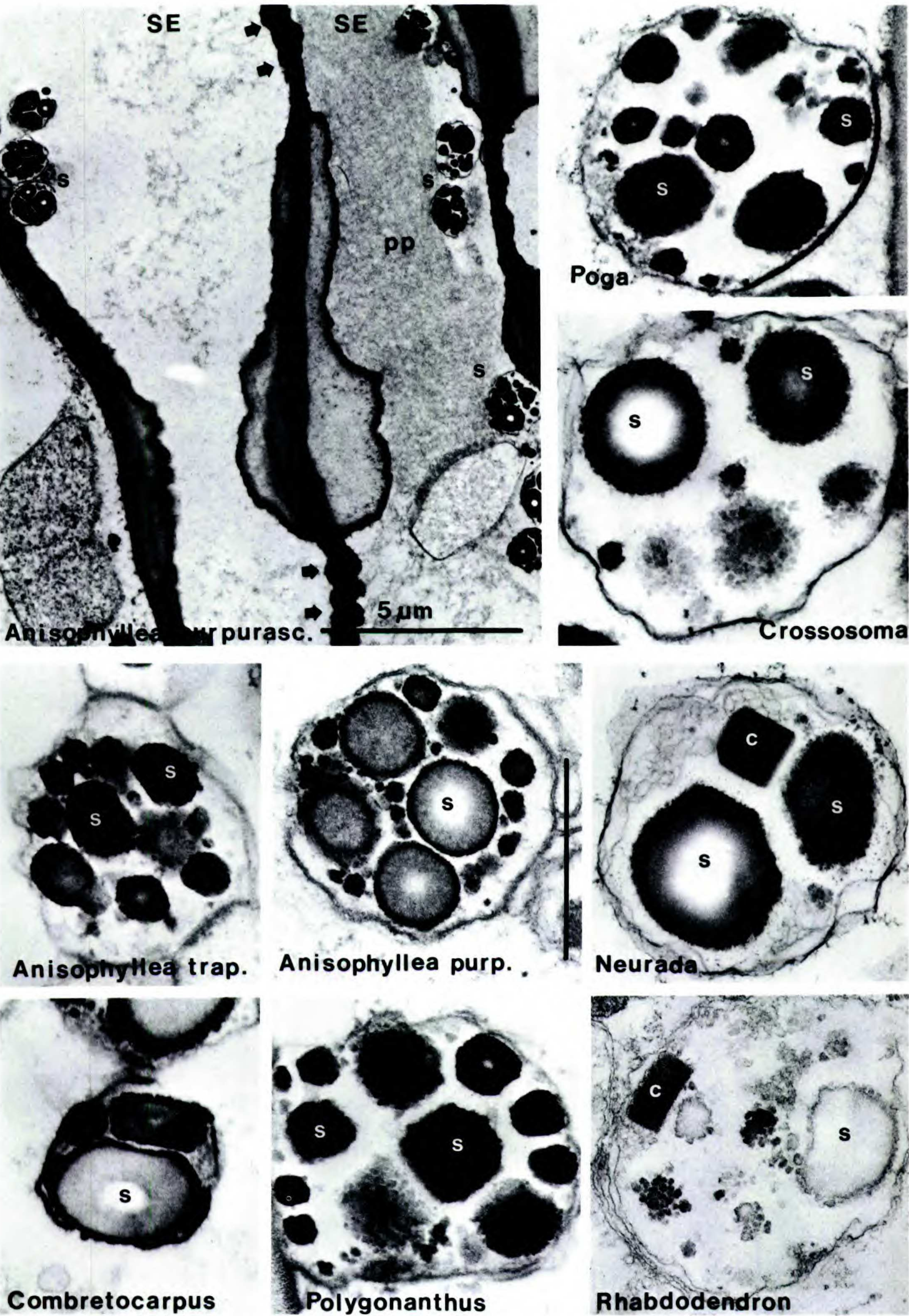
FIGURE 8.   *Upper left: longitudinal section through sieve elements (SE) of* Anisophyllea purpurascens *connected by lateral sieve areas (arrows) and containing many S-type plastids (s)*; ×6,000; pp = *phloem protein. Other*

ized by form-So plastids. Sizes and starch content of the S-type plastids are rather homogeneous. The only exception is *Podostemum*, which has very large plastids (Fig. 7, Table 1) and does not fit into this order, nor in the entire alliance. Cronquist (1981) and Takhtajan (1987) separated the Podostemaceae in its own order. Thorne (1983) placed this family within his Saxifragineae. Until further evidence from other characters emerges, we prefer the treatment as a separate order, somewhat peripheral to the Saxifragales/Rosales.

ROSALES

S-type sieve-element plastids are recorded except for the two families Neuradaceae and Rhabdodendraceae. The pattern of the S-type plastids (diameter and starch content) is similar to that of the Saxifragales. One family includes form-So plastids: the Rosaceae. The presence of these So plastids in at least some genera (see Table 1 for details, e.g., smaller diameter) makes the Rosaceae s. str. distinct from the Malaceae and Amygdalaceae. The plastid pattern of the latter family is not different from that of the S-type genera in the Rosaceae.

Sieve-element plastids of the four genera tested from the Anisophylleaceae display a rather uniform pattern: while their sizes conform with that of both Saxifragales and Rosales, the amount of starch within a plastid is much higher than in the other taxa (cf. Figs. 7, 8). Therefore, on account of the plastid data, an association of Anisophylleaceae with either Saxifragales or Rosales is not excluded, but a positive decision cannot be made.

The remaining two P-type families of Rosales both contain Psc sieve-element plastids, but of different pattern.

Rhabdodendraceae contain in their sieve-element plastids a tiny rectangular protein crystal and up to five irregular starch grains, a pattern repeatedly found within the Magnoliiflorae (see Behnke, 1988).

Neurada is more distinct because of its larger crystal (diameter 0.4 μm) and higher starch content. Its sieve-element plastids come very close to those of the Gunneraceae (see Behnke, 1986b).

CONCLUSIONS DRAWN FROM
THE PLASTID DATA

Given the periphery of families and orders around the Rhizophoraceae—including a few additional ones discussed during the preparation of this Rhizophoraceae symposium—and the distribution of types and forms of sieve-element plastids, the following annotations to the relationships between the different taxa can be made.

The ordinal placement of the Aniosphylleaceae. This is still uncertain as far as sieve-element plastids are concerned. Pattern similarities exist to S-type plastids in the Saxifragales–Rosales groups (not to the Cunoniales), but affinities to other taxa are not ruled out.

If a closer relation to the Rhizophoraceae is still considered, the diameter of the plastids (average of 1.3 μm in both families) would be the only supporting plastid data; otherwise their contents, as discussed, differ by at least two evolutionary steps.

The ordinal placement of the Rhizophoraceae. The identical sieve-element plastids in Rhizophoraceae and Erythroxylaceae, together with the fact that within the dicotyledons the form-P5c is exclusive to these two families, strongly favors their close alliance (see also the ordinal restriction of the subtype-P3 sieve-element plastids, Behnke, 1976b). Related plastid forms are found in the Cyrillaceae (P5cf) and the Humiriaceae (P5cs).

Sieve-element plastids of the Cyrillaceae are distinguished from those of the Rhizophoraceae by the presence of protein filaments in addition to protein crystals (Behnke, 1982a) and a larger diameter (average of 1.6 μm). Nevertheless, their similarity is reason enough to propose at least distant relationships. Traditionally, Cyrillaceae have been placed into Celastrales, Theales, and (recently more often) Ericales (cf. Behnke, 1982a). In view of Dahlgren's (this volume) proposal to associate closely the Rhizophoraceae with the Celastraceae, the inclusion of the Cyrillaceae within the Celastrales (see e.g., Melchior, 1964) may be worth reconsidering.

←

*photographs show S-type sieve-element plastids in the five investigated species of Anisophylleaceae (*A. trapezoidales, A. purpurascens, Combretocarpus motleyi, Polygonanthus amazonicus, Poga oleosa*) and of* Crossosoma bigelovii, *as well as form-Pc plastids of* Neurada procumbens *and* Rhabdodendron macrophyllum. *All* ×30,000. c = *protein crystals*, s = *starch grains. Scale bar = 1 μm.*
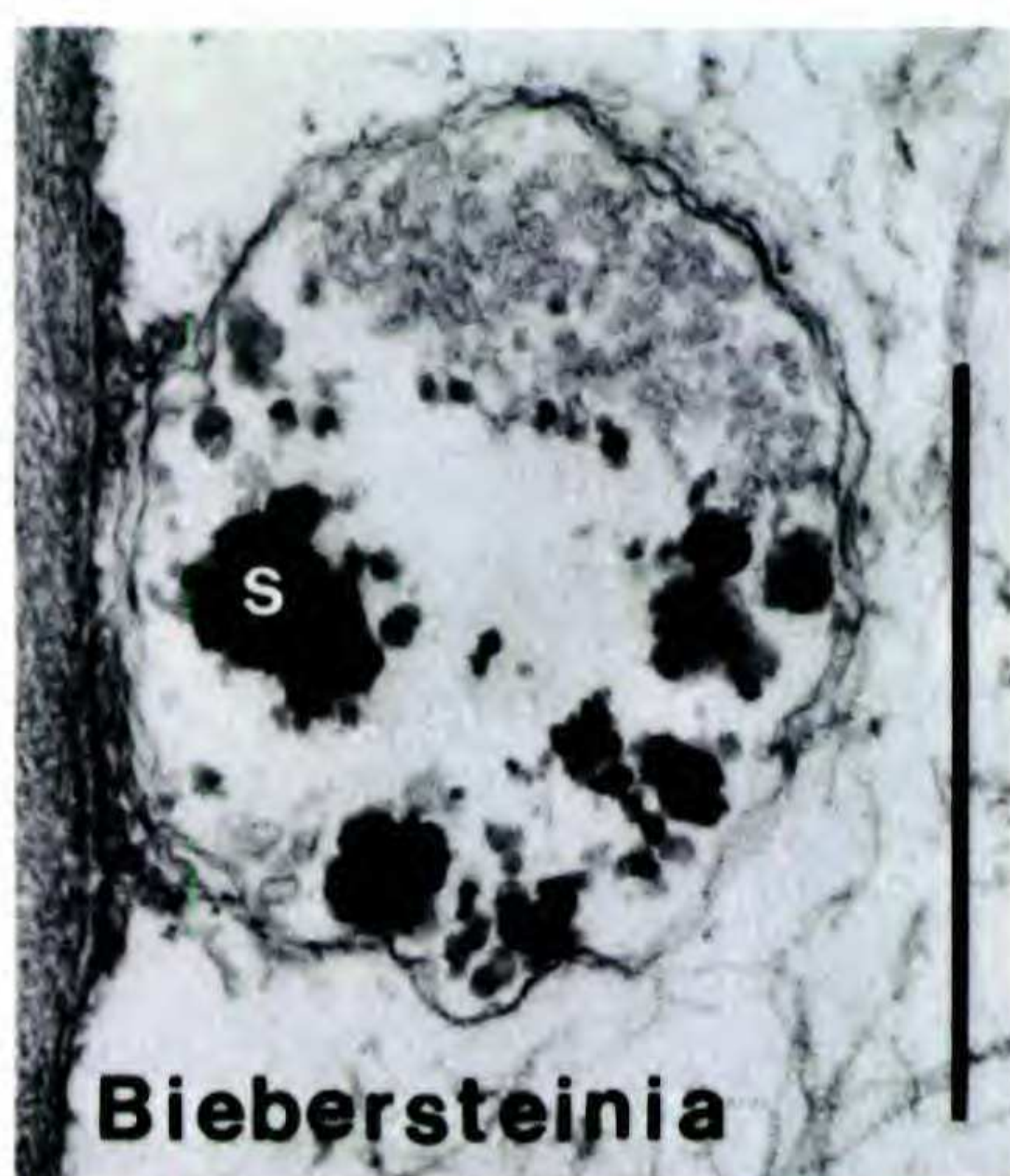
FIGURE 9. *S-type sieve-element plastid of* Bieber-steinia multifida. ×30,000. s = starch grain. Scale bar = 1 μm.

The first and only record for form-P5cs plastids in the Humiriaceae links the form-P5c plastids of the Rhizophoraceae and Erythroxylaceae to the S-type families in the Geraniales s.l. It has further potential in bridging the entire subtype-P5 to the subtype-P4 of the Fabales, thus making the sub-type-P4/P5 a characteristic pattern of sieve-element plastids restricted to the Rutinae (sensu Dahl-gren, this volume).

The form-P5cs plastids found in the Humiri-aceae connect the form-P5c to the S-type plastids in the Geraniales: their number of protein crystals (more than ten on average) is the second highest recorded in the dicotyledons (after those in RHZ and ERY), their number of starch grains and av-erage plastid diameter are compatible with the S-type plastids in the Geraniales. The shape of the protein crystals is not as distinctly rectangular as in the form-P5c plastids (cf. Figs. 2, 5), but even within *Rhizophora* the crystals have no sharp edges (Fig. 5).

The P5cs pattern is very close to that of the form-P4cs plastids present in the Fabales: both contain five or more irregular protein crystals in addition to a variable number of starch grains. It is suggested that from a common ancestor with the plastid inheritance several parallel lines lead to Fabales, Geraniales, Rhizophorales, and probably Celastrales.

However, data from sieve-element plastids do not contribute to the placement of Celastrales un-less the inclusion of the Cyrillaceae (cf. Hutchinson, 1959; Melchior, 1964) is followed.

Dahlgren transferred Elaeocarpaceae from Mal-vales to either the newly defined Celastrales (Dahl-gren, this volume: together with RHZ and CEL) or to his Rhizophorales (Dahlgren, in press: as

the only other family of this order in addition to the RHZ). The data from sieve-element plastids support neither of the two arrangements. However, another phloem character corroborates the exclu-sion of Elaeocarpaceae from the Malvales: Bom-bacaceae, Malvaceae, Sterculiaceae, and Tiliaceae have within their sieve elements so-called persis-tent, crystalline p-protein bodies, which are absent from the Elaeocarpaceae. The persistent p-protein bodies are a typical character of the Malvanae/Violanae and a few other taxa (see Behnke, 1981).

In summary, data from sieve-element plastids suggest the following parallel sequences of families (those not yet investigated are in parentheses; cf. Table 2):

1. Balanitaceae, Zygophyllaceae, Nitrariaceae, Peganaceae, Geraniaceae, Vivianiaceae, Le-docarpaceae, (Biebersteiniaceae), (Dirach-maceae)
2. Linaceae, Hugoniaceae, (Ctenolophona-ceae), Ixonanthaceae
   2.1 Lepidobotryaceae, Hypseocharitaceae, Oxalidaceae, Averrhoaceae
   2.2 Humiriaceae, Erythroxylaceae
      2.2.1 Rhizophoraceae
3. Celastraceae, Elaeocarpaceae
4. Cyrillaceae

Families excluded. On the basis of the sieve-element characters two families discussed during the preparation for this symposium as putative allies are to be definitely excluded: the Flacourti-aceae and Podostemaceae.

The Flacourtiaceae contain S-type sieve-ele-ment plastids, but their persistent p-protein bodies (cf. Behnke, 1981) place them in the Violales.

Podostemaceae differ from the discussed orders by their large S-type plastids and the pattern of starch grains.

NOTE ADDED IN PROOF

Fresh rhizomes of *Biebersteinia multifida* DC. kindly have been made available by E. Gabrielian (Erevan, USSR). The following paragraph should be read after Ledocarpaceae (on page 1389):

Biebersteiniaceae (BBS; Fig. 9) *Biebersteinia multifida* contains S-type plastids with one or few globular starch grains, often disintegrated into tiny particles. The plastid diameter is 1.2 μm.

LITERATURE CITED

BEHNKE, H.-D. 1974 [1975]. P- und S-Typ Siebele-ment-Plastiden bei Rhamnales. Beitr. Biol. Pflanzen 50: 457–464.
———. 1976a. Sieve-element plastids of *Fouquieria*,

Frankenia (Tamaricales), and *Rhabdodenron* (Rutaceae), taxa sometimes allied with Centrospermae (Caryophyllales). Taxon 25: 265–268.

―――. 1976b. Ultrastructure of sieve-element plastids in Caryophyllales (Centrospermae), evidence for the delimitation and classification of the order. Pl. Syst. Evol. 126: 31–54.

―――. 1981. Sieve-element characters. Nordic J. Bot. 1: 381–400.

―――. 1982a. Sieve-element plastids of Cyrillaceae, Erythroxylaceae and Rhizophoraceae: description and significance of subtype PV plastids. Pl. Syst. Evol. 141: 31–39.

―――. 1982b. Sieve-element plastids, exine sculpturing and the systematic affinities of the Buxaceae. Pl. Syst. Evol. 139: 257–266.

―――. 1982c. Sieve-element plastids of Connaraceae and Oxalidaceae. A contribution to the knowledge of P-type plastids in dicotyledons and their significance. Bot. Jahrb. Syst. 103: 1–8.

―――. 1984. Ultrastructure of sieve-element plastids of Myrtales and allied groups. Ann. Missouri Bot. Gard. 71: 824–831.

―――. 1985. Contributions to the knowledge of P-type sieve-element plastids in dicotyledons. II. Eucryphiaceae. Taxon 34: 607–610.

―――. 1986a. Contributions to the knowledge of P-type sieve-element plastids in dicotyledons. IV. Acanthaceae. Bot. Jahrb. Syst. 106: 499–510.

―――. 1986b. Contributions to the knowledge of sieve-element plastids in Gunneraceae and allied families. Pl. Syst. Evol. 151: 215–222.

―――. 1988. Sieve element plastids, phloem-protein and evolution of the flowering plants: III. Magnoliidae. Taxon 37: 699–732.

―――― & T. J. MABRY. 1977. S-type sieve-element plastids and anthocyanins in Vivianiaceae: evidence against its inclusion into Centrospermae. Pl. Syst. Evol. 126: 371–375.

―――― & L. POP. 1981. Sieve-element plastids and crystalline P(hloem)-protein in Leguminosae: micro-

morphological characters as an aid to the circumscription of the family and subfamilies. Pp. 707–715 *in* R. M. Polhill & P. H. Raven (editors), Advances in Legume Systematics. Academic Press, London.

BUVAT, R. 1963. Les infrastructures et la différenciation des cellules criblées de *Cucurbita pepo* L. Portugaliae Acta Biol., Ser. A, 7: 249–299.

CRONQUIST, A. 1981. An Integrated System of Classification of Flowering Plants. Columbia Univ. Press, New York.

DAHLGREN, G. The last Dahlgrenogram—System of classification of the Dicotyledons. *In:* K. Tan (editor), The Davis and Hedge Festschrift. Edinburgh Univ. Press. (In press.)

DAHLGREN, R. 1983. General aspects of angiosperm evolution and macrosystematics. Nordic J. Bot. 3: 119–149.

―――. Rhizophoraceae and Anisophylleaceae: summary statement, relationships. Ann. Missouri Bot. Gard. (this volume).

ESAU, K. & J. CRONSHAW. 1968. Plastids and mitochondria in the phloem of *Cucurbita*. Canad. J. Bot. 46: 877–880.

HUTCHINSON, J. 1959. The Families of Flowering Plants. 2 volumes. Academic Press, London & New York.

MELCHIOR, H. (editor). 1964. A. Engler's Syllabus der Pflanzenfamilien, Band II, 12th edition. Borntäger, Berlin.

TAKHTAJAN, A. 1987. Systema Magnoliophytorum. Nauka, Leningrad. [In Russian.]

THORNE, R. F. 1983. Proposed new realignments in the angiosperms. Nordic J. Bot. 3: 85–117.

TOBE, H. & P. H. RAVEN. 1987. Systematic embryology of the Anisophylleaceae. Ann. Missouri Bot. Gard. 74: 1–26.

WEBER, W. A. 1982. Mnemonic three-letter acronyms for the families of vascular plants: a device for more effective herbarium curation. Taxon 31: 74–88.